PLATOMA ARDREANUM (SCHIZYMENIACEAE, GIGARTINALES) AND *HALYMENIA CHIANGIANA* (HALYMENIACEAE, HALYMENIALES), TWO NEW SPECIES OF PROLIFEROUS, FOLIOSE RED ALGAE FROM THE HAWAIIAN ISLANDS

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ABSTRACT — Two superficially similar foliose algae with extensively ruffled surfaces are described as new species from the Hawaiian Islands. *Platoma ardreanum* Kraft *et* Abbott, sp. nov., is known from drift and shallow-subtidal reef flats and is the first central-Pacific member of its genus to be reliably reported. Plants are characterized by: 1) lobed to dentate non-stipitate blades anchored by one to several crustose holdfasts; 2) numerous "calluses" along lower blade margins; 3) conspicuous intercalary "gland" cells; 4) monoecious gametophytes; spermatangia borne in patches on outer-cortical mother cells; 5) 3(-4)-celled carpogonial branches, the basal cell of which often bears a 1- or 2-celled lateral; 6) supporting and epi-supporting cells that also bear 1- or 2-celled laterals; 7) the longitudinal division of the presumably fertilized carpogonium, each half of which forms a stout fusion to an epi-supporting cell; 8) the growth of one or more connecting-filament organizing cells and the subsequent production of multiple branched, septate connecting filaments from just one of the two contacted epi-supporting cells; 9) the septation of the connecting filament at its point of contact to the lateral surface of the auxiliary cell and the ongrowth of the connecting filament to effect further diploidizations; and 10) non-ostiolate cystocarps. Features of the new species are compared to those of the closest apparent relative, *Platoma izunosimensis* Segawa, from southern Japan.

Halymenia chiangiana Abbott *et* Kraft, sp. nov., known from drift and rare attached collections, is characterized by: 1) extensively ruffled and lobed blade surfaces and margins; 2) a filamentous medulla with stellate inner cortical cells and frequent refractive "ganglioid" medullary cells; 3) occasional medullary filaments that traverse the medulla to link the opposite inner cortexes; 4) more-or-less flattened auxiliary-cell ampullae composed of sparingly branched filaments that surround the base of an ostiole formed prior to diploidization of the intercalary auxiliary cell; 5) gonimoblasts developing on auxiliary cells that fuse not at all or only slightly with adjoining ampullar cells; and 6) tetrasporangia immersed in a modified cortex of anticlinal filaments. Comparison is made to previously described *Halymenia* species from the western Pacific.

RÉSUMÉ — Deux algues foliacées, très semblables d'aspect au premier coup d'oeil et toutes deux présentant une surface très frippée, sont décrites comme espèces nouvelles des îles Hawaï. *Platoma ardreanum* Kraft *et* Abbott, sp. nov., est connu en épave et de plateaux récifaux infralittoraux peu profonds. C'est la première fois qu'un membre de ce genre est signalé de manière fiable pour la région centre-Pacifique. Les thalles sont caractérisés par: 1) des lames lobées à dentées, dépourvues de stipe et fixées par une ou plusieurs bases en forme de croûte ; 2) de nombreux « cals » le long des marges

inférieures des lames ; 3) des cellules « glandulaires » intercalaires caractéristiques ; 4) des gamétophytes monoïques ; des spermatocystes en amas provenant d'une cellule-mère corticale externe ; 5) un rameau carpogonial constitué de 3(-4) cellules et dont la cellule basale porte souvent des rameaux latéraux constitués d'une ou deux cellules ; 6) la cellule support et les cellules situées juste au-dessus de celle-ci (*epi-supporting cells*) portant souvent aussi de tels rameaux ; 7) la division longitudinale du carpogone supposé fécondé dont chaque moitié fusionne solidement avec une *epi-supporting cells* ; 8) la croissance d'une ou plusieurs cellules productrices de filaments de jonction et la production qui en résulte de filaments de jonctions cloisonnés et plusieurs fois ramifiés, à partir de seulement d'une ou des deux *epi-supporting cells* contactées ; 9) le cloisonnement du filament de jonction à son point de contact avec la surface latérale de la cellule auxiliaire et l'extension du filament de jonction qui permettra d'effectuer des diploïdisations supplémentaires ; 10) des cystocarpes sans ostiole. Les caractéristiques de la nouvelle espèce sont comparées à celles de l'espèce apparemment la plus proche: *Platoma izunosimensis* Segawa du sud du Japon.

Halymenia chiangiana Abbott *et* Kraft, sp. nov., connu en épave et de quelques rares récoltes en place, est caractérisé par 1) des lames lobées à la surface et aux marges très frippées ; 2) une moelle filamenteuse avec des cellules corticales internes étoilées et des cellules médullaires « glanglioïdes » réfringentes fréquentes ; 3) des filaments médullaires occasionnels traversant la moelle pour relier les deux parties opposées du cortex interne ; 4) une cellule auxiliaire plus ou moins aplatie, dans l'*ampulla*, cette dernière composée de filaments peu ramifiés qui entourent une ostiole formée avant la diploïdisation de la cellule auxiliaire intercalaire ; 5) des gonimoblastes se développant sur des cellules auxiliaires qui ne fusionnent que légèrement ou pas du tout avec les cellules adjacentes de l'*ampulla* ; 6) enfin, par des tétrasporocystes enfoncés dans un cortex modifié, formé par des filaments anticlinaux. Cette espèce nouvelle est comparée aux autres espèces du genre *Halymenia* décrites du Pacifique occidental. (Traduit par la Rédaction)

KEY WORDS: marine algae, Rhodophyta, Gigartinales, Nemastomataceae, Schizymeniaceae, *Halymenia*, *H. chiangiana*, *Platoma*, *P. ardreanum*, Hawaiian Islands, taxonomy, new species.

INTRODUCTION

Two marine species of superficially similar habit have been recognized during preparation by one of us (IAA) of a comprehensive Hawaiian red-algal flora. Internal anatomy shows them to be undescribed representatives of separate families and orders and to exemplify important reproductive features distinctive of their respective genera. Although these algae have been only infrequently collected, they are attractive plants that can reach substantial dimensions.

The first species that we describe, *Platoma ardreanum* Kraft *et* Abbott, sp. nov., has been known for several years and provisionally treated as a member of the Nemastomataceae, a family of the Gigartinales for the most part infrequently recorded from tropical regions (Kraft & John, 1976; Kraft, 1984).

Members of the Nemastomataceae [1] have been considered by some writers to be among the least vegetatively and reproductively specialized members of the order Gigartinales (Kylin, 1932, 1956; Kraft, 1975, 1981). This conclusion is largely based on the fact that fronds internally consist of laxly organized, strictly di- or trichotomous filaments lacking secondary pit-connections between cells (the genus *Schizymenia* being the sole exception on both counts), as well as carposporophytes that are embedded, compact structures in which virtually every cell differentiates into a carposporangium. Kraft (1981) argued for the relatively primitive state of this non-procarpic family, not just within the

1. Also referred to as the Nemastomaceae or Gymnophloeaceae.

Gigartinales but the Florideophycideae as a whole, partly on the grounds that single fertilizations, which seem to be rare events in many species, tend to vastly multiply their effects through the production of large numbers of connecting filaments and the sequential diploidization of many auxiliary cells, resulting in numerous gonimoblasts that may be dispersed widely throughout the gametophyte. These phenomena stood in seeming contrast to the one-to-one correlation of fertilizations to carposporophytes that take place in procarpic families, particularly the Ceramiales. We now know from investigations of gene sequences (Ragan *et al.*, 1994; Freshwater *et al.*, 1994; Saunders & Kraft, 1996, submitted) that the evolutionary picture of florideophycidean orders and families does not correlate very well with any particular type of carposporophyte structure, although the genus *Schizymenia* appears to occupy a position near the base of the gigartinalean clade.

The image painted by Kraft (1981) of the Nemastomataceae as a group of closely allied genera that for the most part has retained its primitive characters from precursors in deep, warm-water habitats was demonstrably wrong even as those speculations were made. Overlooked entirely was the classic work of Berthold (1884, p. 12, 22 pl. 6, figs 2,3,5,8) showing that carpogonia in *Platoma cyclocolpum* (Montagne) Schmitz (as *Nemastoma cervicorne* J. Agardh) first fuse with adjacent nutritive auxiliary cells before connecting filaments are issued, and that both carpogonial branches and auxiliary cells in *Nemastoma dichotoma* J. Agardh are produced on/in adventitious rhizoids rather than "normal" cortical filaments. Had this publication been more carefully heeded, Feldmann (1942), Kylin (1932, 1956) and Kraft & John (1976) would hardly have emphasized such relatively trivial features as the presence or absence of gland cells or of ostioles in their ill-grounded attempts to distinguish species of *Nemastoma* from those of *Platoma*.

With reinvestigations of the respective type species *Nemastoma dichotomum* by Athanasiadis (1988) and *Platoma cyclocolpum* by Masuda & Guiry (1994), the defining features of these two very different genera have become clarified. The works of Ardré (1980), Itono (1984) and Masuda & Guiry (1994) have additionally demonstrated such significant differences between *Schizymenia*, *Titanophora* and *Platoma* and the rest of the Nemastomataceae that these three genera have now been removed to the separate family Schizymeniaceae by Masuda & Guiry (1994). Within the remaining Nemastomataceae, clearer understandings of reproductive processes and life-histories have been made the bases of the additional genera *Tsengia* (Fan & Fan, 1962) and *Itonoa* (Masuda & Guiry, 1995), although much remains to be determined about features of the bulk of the family's actual species. Preliminary molecular data drawn from SSU gene sequences of species of *Schizymenia*, *Platoma* and *Tsengia* by G.W. Saunders (Saunders & Kraft, unpublished) suggest that not only are the members of the Schizymeniaceae far removed at the family level from those of the Nemastomataceae, but that these taxa probably belong to separate orders. Work in several labs is now being directed at determining the phylogenetic positions of the two groups.

The critical study of the type species of *Platoma* by Masuda & Guiry (1994) has at long-last brought the welcome provision of sound criteria for inclusion in that genus, but it also imposes some stiff requirements for often-difficult observations of immediate post-fertilization events. Although only the type and one other of the nine described species have been shown to display the defining features of *Platoma*, for the first time investigations can now be directed with precision to confirming the generic status of "nemastomataceous" species.

The distinctive Hawaiian frondose alga belonging to the Nemastomataceae/Schizymeniaceae complex occurs sporadically in drift or on shallow reef flats in Hawaii.

Until now, we have lacked good criteria and critical stages for determining its true generic placement. With the assistance of Masuda & Guiry's (1994) excellent study and success in finally locating critical post-fertilization stages, it is now possible to describe this entity as the first central-Pacific species of *Platoma*.

The Hawaiian Islands are a volcanic chain located near the northern boundary of its tropical province. Their well-developed coral reefs, which occur on and intermixed with basaltic substrata, support the richest and most diverse marine macroalgal flora of any oceanic island group in the world, as demonstrated by recent monographic studies (Abbott, in press). Particularly well represented are species of liagoroids, Gelidiales, *Gracilaria* and Ceramiales, although those of the Nemastomatceae/Schizymeniaceae complex are comparatively rare. Apart from the new entity we describe below, the Nemastomataceae is represented only by two infrequently encountered species of *Predaea*, and the Schizymeniaceae by a single, rarely collected species of *Titanophora*.

The second new species that we describe, *Halymenia chiangiana* Abbott & Kraft, sp. nov., has only recently come to light in drift and a single *in situ* reef-flat collection, although it is probably a populant of shallow reef flats that also host *Platoma ardreanum*, at least on Maui island. The genera of the Halymeniaceae are widespread from tropical to cold-temperate seas (Womersley & Lewis, 1994), with the greatest concentration being in Australia and the north-eastern Pacific (Lewis & Kraft, 1992). Long regarded as the type family of the order Cryptonemiales (either as it is designated today, the Halymeniaceae, or previously as the Grateloupiaceae (Kylin, 1956) or Cryptonemiaceae (Chiang, 1970)), the Halymeniaceae was incorporated into the Gigartinales by Kraft & Robins (1985) when they challenged the validity of the classical criteria by which the Cryptonemiales was defined, then was re-elevated as the type family of the order Halymeniales by Saunders & Kraft (1986) based on analyses of SSU-gene sequences.

The Hawaiian Islands are relatively rich in members of the Halymeniaceae, where seven genera and fourteen species are recorded (Abbott, in press). Nevertheless, broadly foliose representatives are rare, most being (sub-)dichotomous to pinnate and narrowly linear. The species that we now describe differs from all others in the breadth and thickness of its fronds, and particularly in the profuse covering of ruffles, lobes and excrescences on the blade surfaces.

Platoma ardreanum Kraft *et* Abbott, sp. nov.

Plantae foliosae, orbiculatae ad profunde fissae, marginibus dentatis vel lobatis; paginis laminarum distalium projecturis acutis et obtusis late obductis. Laminae affixae per primarium crustaceum hapteron et aliquot secundaria haptera formata ad margines basales. Cortex moniliformis, numerosos intercalares glandicellula continens. Planta monoica. Spermatangia in superficiaribus pannis. Rami carpogoniales tricellulares, cellula basalis plerumque uni-vel bicellulari sterili laterali ramo. Cellulae fulcrantes, cellulae epi-fulcrantes et cellulae proxime portatae in cellulis epi-fulcrantibus unum vel plures cellulas steriles ante fecundationem procreantes, cellulae laterales cellulis parentibus saepe conjungentes. Carpogonium post fecundationem oblique dimidiatum, ambo dimidia ad contiguam cellulam epi-fulcrantem conjungentia, una ex quibus producit primas cellulas filorum eonjunctivorum ex quibus numerosa, ramosa, septata fila conjunctiva crescunt. Cellulae auxiliares intercalares in fasciculo corticali separato, distinguibiles antequam recipiens nucleum diploideum. Nucleus diploideus in inferiore latere cellulae auxiliaris in loco conjunctionis filo conjunctivo iniens, filum conjunctivum tum dividens, crescens porro et peragrans, iterum atque iterum conjungens itidem et nucleum diploideum donans. Prima cellula gonimoblasti apicalis in

cellula auxilari, in duas primas cellulas gonimolobi dividens. Cystocarpia sine ostiolo, 80-120 μm diam., ex carposporangiis omnino constata. Tetrasporangia incognita.

Diagnosis. Plants foliose, dentate or lobed at the margins, with mature surfaces extensively covered with narrowly to bluntly rounded projections. Blades sessile, attached by a primary crustose holdfast and several secondary holdfasts formed along the basal margins. Wart-like calluses also formed along the basal margins of most specimens. Cortex moniliform, containing numerous intercalary gland cells. Plants monoecious (protandrous). Spermatangia in superficial patches. Carpogonial branches 3(-4)-celled, the basal cell usually with a one- or two-celled sterile lateral branch. Supporting cells, epi-supporting cells and cells immediately borne on epi-supporting cells producing one or more sterile cells prior to fertilization, the lateral cells often fusing back onto their parent cells. Fertilized carpogonium dividing in two obliquely, both halves fusing to an adjacent epi-supporting cell, one of which produces connecting-filament initial cells from which grow numerous branched, septate connecting filaments. Auxiliary cells intercalary in separate cortical fascicles, distinguishable prior to receiving the diploid nucleus (diploidization). Diploid nucleus entering on the lower side of the auxiliary cell at the point of fusion with the connecting filament, the connecting filament then dividing, growing onwards and effecting further diploidizations. Gonimoblast initials arising distally on auxiliary cells, dividing into two gonimolobe initials. Cystocarps non-ostiolate, 80-120 μm in diam. composed entirely of carposporangia. Tetrasporangia unknown.

Etymology. This species is named in honor of Madame Professor Francoise Ardré, whose meticulous study of reproductive morphology and life history in *Schizymenia dubyi* (Ardré, 1980) is substantially responsible for the ultimate recognition of the Schizymeniaceae as a distinct and separate family of the Gigartinales. The authors are joined in their admiration of Dr Ardré and their good wishes for her retirement years by Dr Karla McDermid, who prepared the Latin diagnosis.

Holotype. MELU, A24,197 (Fig. 1), cystocarpic specimen collected on 28 January 1978 by G. and C. Kraft and K. Schlech. Isotypes and paratypes in BISH and MELU.

Habitat. Most specimens are from drift, although *in situ* Maui collections came from a basaltic reef platform overlain by encrusting Corallinaceae at 1.5-2 m depths.

Hawaiian distribution. 1) Oahu I.: 'Ewa Beach, drift (*G. & C. Kraft, K. Schlech*, 26.xi.1977. MELU, A24189, 24191); (*G. & C. Kraft. K. Schlech*, 28.i.1978. MELU, A24190, 24192-94). 2) Maui I. Ma'alaea, from a basalt groin near the sandy beach about 300 m east of the harbor at 1.5-2 m depths (*L. M. Hodgson*, 14.iv.1996. BISH, 1A22787); (*G.T. Kraft*, 28.v.1996. MELU, K10641).

World distribution. Recorded only from the Hawaiian Islands.

Vegetative structure. Plants are foliose, the largest broader than tall, 11 x 16.5 cm, 250-500 μm in thickness, and are initially anchored by a single, sessile, crustose holdfast, later by a series of holdfasts scattered along the basal margin. Hard, whitish "calluses" 1-2 mm in diam. by 700-1000 μm in thickness and composed of dense aggregations of longitudinally aligned filaments are also present to some degree along the basal margins of most fronds (Figs 4, 5) but are not associated with the holdfasts. Blades are deep reddish-brown in color, entire and nearly orbicular when young, the margins lined by acute dentitions or blunt narrow lobes, the fronds becoming deeply incised and broadly lobed with maturity and tending to spread in two roughly equal "wings" from the central holdfast area (Figs 1, 2). Surfaces of the blades are smooth basally (Figs 2, 4) but at fairly

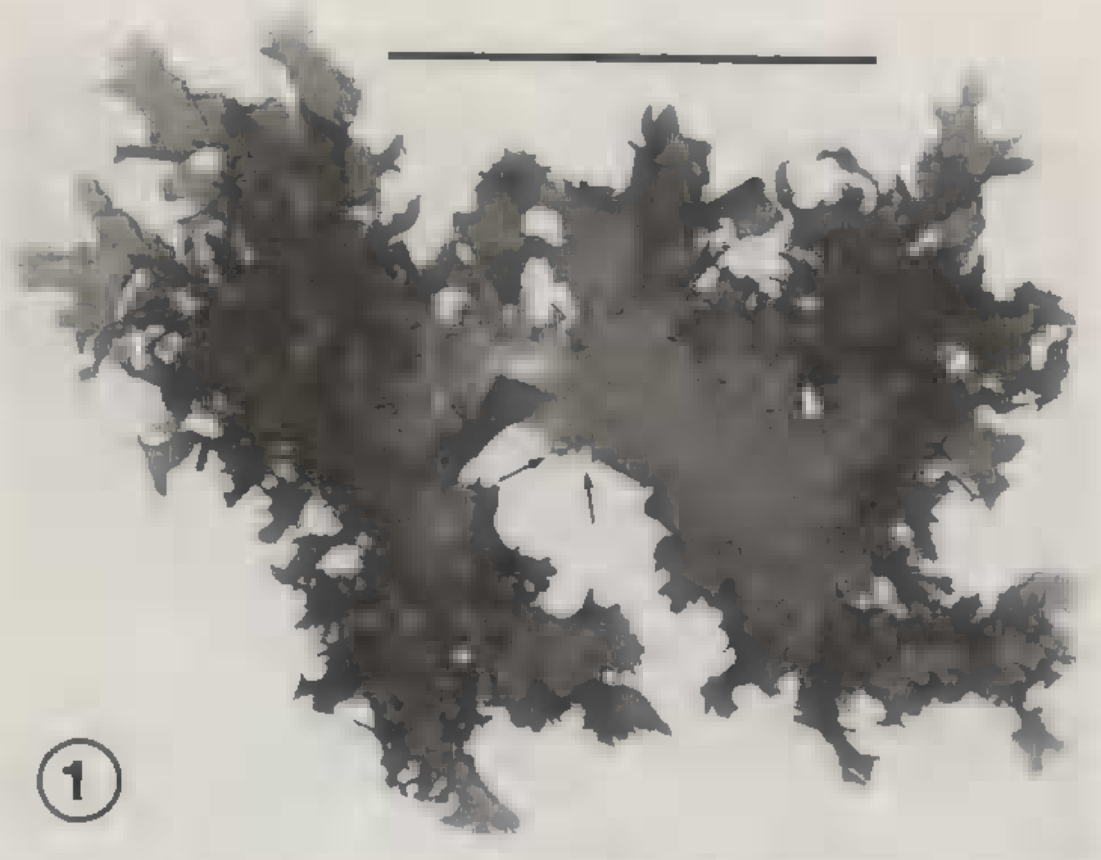


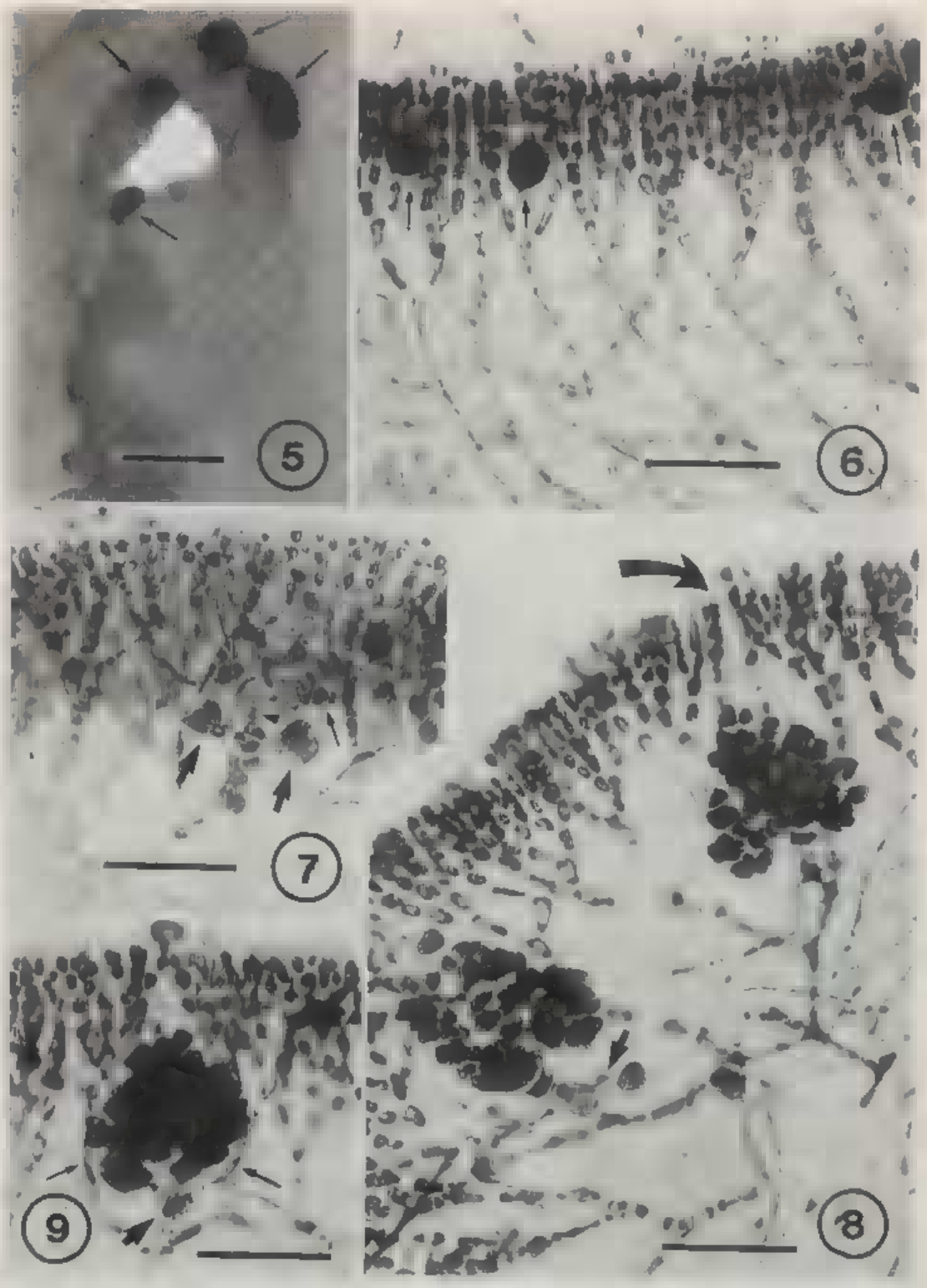
Fig. 1. *Platoma ardreanum* Kraft *et* Abbott sp. nov. Habit of the cystocarpic holotype specimen (MELU, A24,197), the blade sessile on two holdfast pads (arrows). Scale = 5 cm.

even distances from the holdfasts become covered distally with large numbers of blunt lobes and ruffles (Figs 1, 2, 5) that give the fronds soft, distinctively tripe-like textures and apearances.

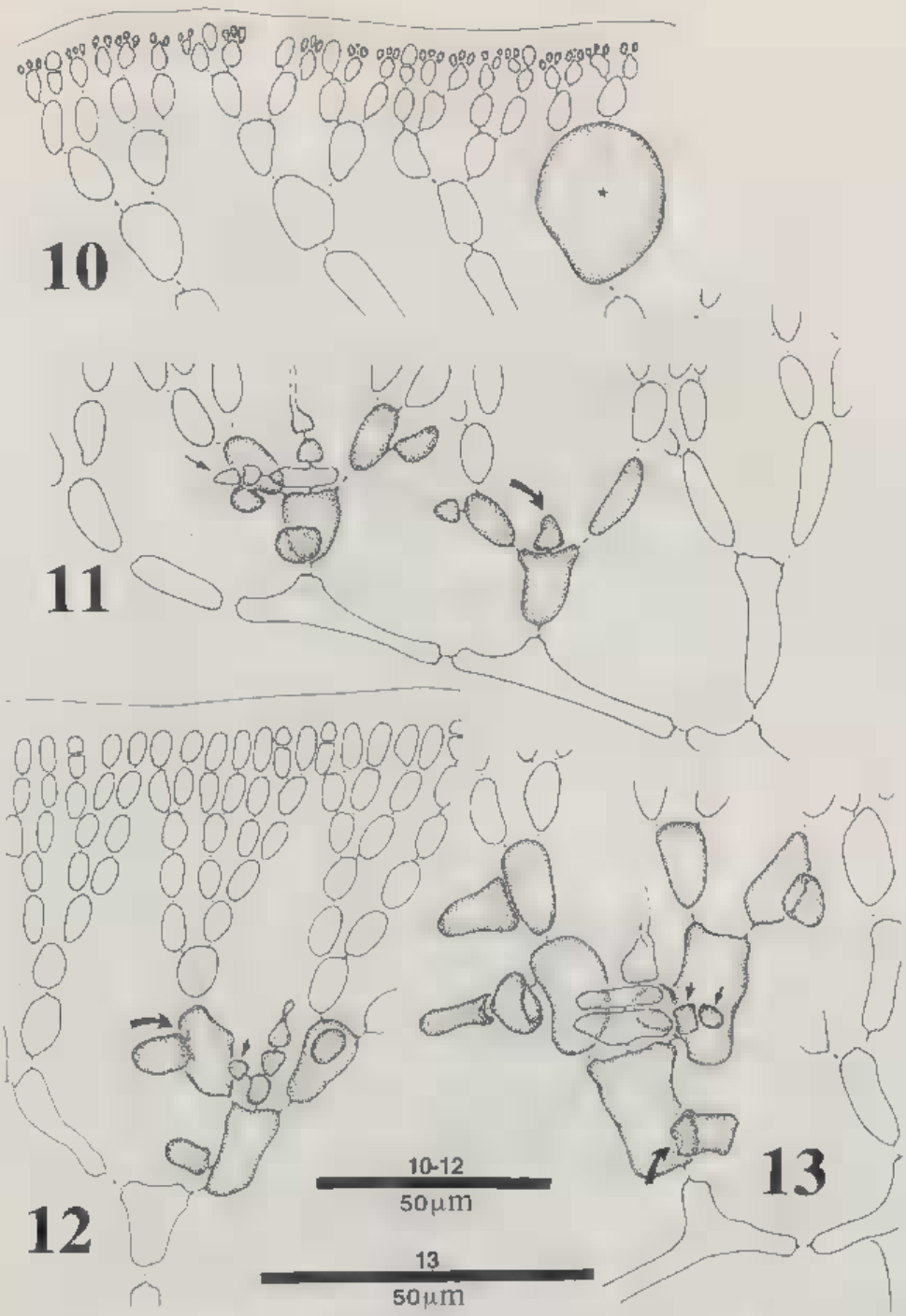
Medullary filaments are sparse in the central gelatinous matrix, mostly periclinally oriented, and consist of a mixture of primary filaments and rhizoids, most 2.5-3 µm in diam., with occasional filaments 5-7(-13) µm wide composed of cells up to 200 µm in length. The cortex is 60-100 µm deep and composed internally of repeatedly dichotomous, regularly spaced filaments (Fig. 6), the cells elongate and 10-22 µm in length in the inner layers, ovoid and 4-10 µm long in the outer layers. Spherical to obovate or obpyriform intercalary gland cells 12-20 µm by 12-17 µm are scattered and usually frequent in the cortex (Figs 6, 10), the contents staining preferentially in aniline blue.

Reproduction. Plants are monoecious (protandrous), the spermatangia ovoid, 2-4 µm in diam., and cut from mother cells occupying broad patches of the blade surfaces (Fig. 10). Carpogonial branches are three-(rarely 4)-celled and borne in the axils of inner cortical-filament dichotomies (Fig. 11), the basal cells usually bearing a one- (Fig. 12) or two-celled sterile lateral and often being conspicuously transversely elongate (Figs 11, 13). The supporting cell, the two cells immediately borne on the supporting cell (epi-supporting cells) and often the cells borne on the epi-supporting cells usually cut off a single lateral cell

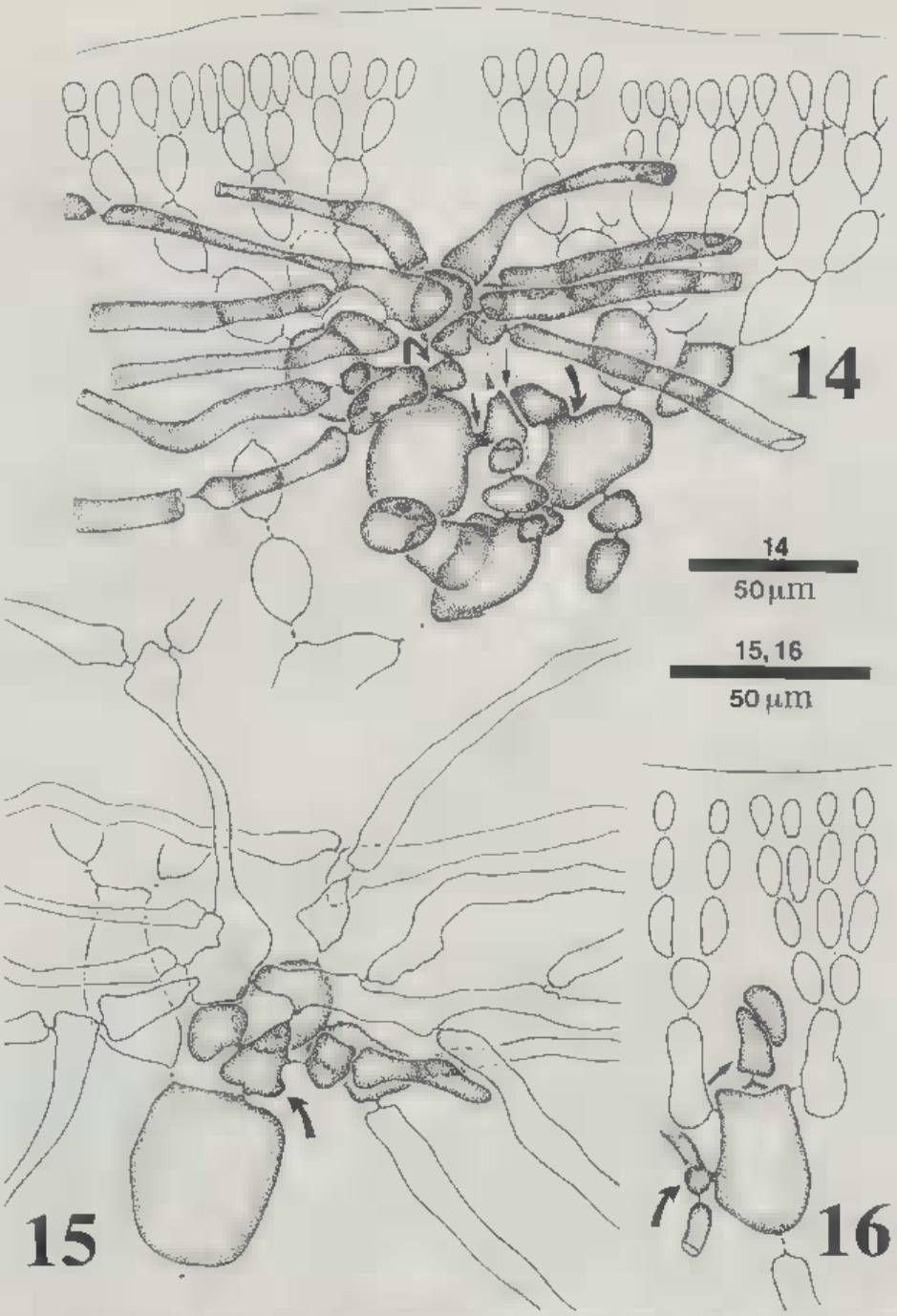
Figs 2-4. *Platoma ardreanum* Kraft *et* Abbott sp. nov. Fig. 2. Habit of a large sterile specimen anchored by two closely positioned holdfasts (arrow) (MELU, A24,189). Scale = 5 cm. Figs 3, 4. Habit of wet-preserved blades (MELU, K10641). 3. Clusters of blades and blade lobes adjacent to the basal holdfast (arrow). Scale = 10 mm. Fig. 4. Portion of the frond showing proximally smooth and distally ruffled blade, and the calluses (arrows) lining a lower margin. Scale = 5 mm.



Figs 5-9. *Platoma ardreanum* Kraft *et* Abbott sp. nov. Fig. 5. Detail of the calluses (arrows) borne along the lower margin of the blade in Fig. 4. Scale = 2 mm. Fig. 6. Frond trans-section showing "gland" cells (arrows) at the border between the lax medullary filaments and the anticlinal outer cortex. Scale = 50 µm. Fig. 7. A carpogonial branch and carpogonium (arrowhead) flanked by epi-supporting cells (large arrows) on an inner cortical supporting cell. Cells on the epi-supporting cells bear 1- and 2-celled adventitious laterals (small arrows). Scale = 50 µm.
Fig. 8. Two carposporophytes, one borne on an auxiliary cell to which a remnant of the connecting filament (straight arrow) is attached, the other forcing a break in the cortex (curved arrow), presumably effecting spore release. Scale = 50 µm. Fig. 9. A mature carposporophyte flanked by two slender involucral cells (small arrows), all three borne on an inner-cortical auxiliary cell (large arrow). Scale = 50 µm.



Figs 10-13. *Platoma ardreamum* Kraft *et* Abbott sp. nov. Fig. 10. Spermatangia (stippled) borne in pairs and threes on surface mother cells of a cortex segment that contains an intercalary gland cell (starred). Fig. 11. A carpogonial-branch primordium (curved arrow) and a mature carpogonial branch, the latter with a basal cell bearing a two-celled lateral (straight arrow). The supporting cell and epi-supporting cells also bear single-celled laterals. Fig. 12. An immature carpogonial branch with a single-celled lateral on the basal cell (straight arrow) and flanked by epi-supporting cells, on one of which the single-celled lateral is fusing back (curved arrow). Fig. 13. A three-celled carpogonial branch composed of transversely elongate basal and hypogynous cells, the basal cell bearing a two-celled lateral (straight arrows). The single-celled lateral on the supporting cell is fusing back onto it (curved arrow), and cells distal to the supporting cell bear 1- and 2-celled laterals.



Figs 14-16. *Platoma ardreamum* Kraft *et* Abbott sp. nov. Fig. 14. A series of connecting-filament initial cells (bent arrow) issuing large numbers of connecting filaments (stippled) and borne on the distal end of an epi-supporting cell attached (coarse straight arrow) to a derivative of the apparently obliquely divided (thinner straight arrow) fertilized carpogonium. The remainder of the carpogonium is fused (curved arrow) to the other epi-supporting cell, which has not initiated connecting filaments. Fig. 15. An epi-supporting cell bearing a connecting-filament initial cell (arrow) and large numbers of connecting filaments (stippled). Fig. 16. The oblique first division of the gonimoblast initial (straight arrow) on ■ generative auxiliary cell to which remnants of ■ septate connecting filament (curved arrow) are laterally attached.

(occasionally chains of two lateral cells) that may (Figs 12, 13) or may not (Figs 12-14) fuse back onto the parental cells before or after fertilization. Immediate post-fertilization events were not seen, but large numbers of branched, septate connecting filaments issue from one or more connecting-filament organizing cells borne at the distal end of one of the two epi-supporting cells (Figs 14, 15). It appears that the fertilized carpogonium divides in two obliquely (Fig. 14), with each derivative fusing to the most closely adjacent epi-supporting cell. In the one complete post-fertilization stage observed (Fig. 14), only the epi-supporting cell connected to the half of the divided carpogonium to which remnants of the trichogyne were attached gave rise to cells from which connecting cells issued, the other epi-supporting cell seemingly being dormant or perhaps retarded in the production of connecting filaments despite its clear fusion with a carpogonium-derivative cell.

Auxiliary cells are intercalary in inner cortical filaments, swollen and dark-staining before diploidization. Diploidization is achieved by lateral fusion to a connecting filament, which then divides just distal to its point of fusion and grows on to effect presumable further diploidizations (Fig. 16). The gonimoblast initial is apical on the auxiliary cell, the first division of the initial being oblique (Fig. 16). Cystocarps are 80-120 μm in diam. and are generally composed of two distinct gonimolobes with synchronously maturing carposporangia (Fig. 8). Carposporangia are cuboidal, rectilinear or angular, 12-15 by 10-12 μm. The cystocarps are subtended by elongate but otherwise little-modified cortical filaments (Fig. 9) and are non-ostiolate, the cortex above the carposporophyte spreading and finally rupturing as the gonimolobes develop outwardly (Figs 8, 9). Tetrasporophytes are unknown.

DISCUSSION

The closest seeming relative of *Platoma ardreanum* is *P. izunosimensis* Segawa (1938) from southern Japan, the two species being similar in habit although the Japanese representative is not recorded as having the distinctive calluses, the same degree of blade ruffling, or the dentate to narrowly proliferous margins of the Hawaiian collections (Segawa, 1938, pl. 35; Itono, 1984, pls 6, 7). Detailed descriptions of the anatomy and reproductive processes in *P. izunosimensis* were made in an unpublished monograph of Japanese Gigartinales by Itono (1984), who did not depict sterile laterals on either the basal cells of the carpogonial branches or the supporting cells (Itono, 1984, figs 8A, E). Itono demonstrated (1984, figs 8C, D) that following fertilization the carpogonium does not divide in two, but fuses directly with one of the epi-supporting cells and becomes secondarily pit-connected (presumably via the cutting off of a connecting cell) to the other, with both nutritive auxiliary cells issuing multiple connecting filaments from subisodiametric "connecting-filament initial" cells (*sensu* Masuda & Guiry, 1984, figs 11-13). Ardré (1980, pl. 1, figs 5, 6) illustrates a virtually identical process in *Schizymenia*, both Ardré (1980, pl. 1, fig. 6; pl. 2, fig. 12) and Itono (1984, fig. 8D) documenting connecting filaments that issue from both epi-supporting cells. Itono (1984, fig. 8D) additionally shows that connecting filaments can also arise from a cell distal to one of the two epi-supporting cells, to which the carpogonium may in fact also be directly fused. *Titanophora* (Itono 1984), as well as *Platoma*, shows comparable post-fertilization processes, which constitute the major defining features of the family Schizymeniaceae as established by Masuda & Guiry (1995).

The undoubtedly elaborate sequence of events that leads to connecting-filament production in *Platoma ardreanum* thus appears to yield a somewhat different result from

those documented in the few other species of Schizymeniaceae studied to date. The oblique division of the carpogonium and the direct fusion of both halves with nutritive auxiliary cells, as well as the seeming restriction of connecting-filament initial cells to only one of the two nutritive auxiliary cells, set the Hawaiian species apart. These features have been seen only twice in our slide preparations, however, and it is therefore not known how consistent these post-fertilization phenomena are. Such questions remain unanswered for all Schizymeniaceae.

Where the Hawaiian species fits phylogenetically is pure speculation at the moment in the absence of comparative molecular data, although Masuda & Guiry's (1994) depiction of the European type species as lacking any sterile cells on the carpogonial branch, supporting cell or epi-supporting cells may indicate that it is a more recently evolved entity than the two subtropical-Pacific species. In terms of the abundance of sterile cells in the carpogonial apparatus of *P. ardreanum*, the illustrations of Ardré (1980, pl. 1, figs 3-5) showing sterile cells/filaments on the basal and supporting cells of the type species of *Schizymenia* suggest that *Schizymenia* is more like *Platoma ardreanum* in this regard than are either *P. cyclocolpum* or *P. izunosimensis*. Sterile cells and filaments may thus have relevance in characterizing species but not great import at the genus level.

Platoma ardreanum joins *P. cyclocolpum* and *P. izunosimensis* in displaying the vegetative and reproductive criteria advanced by Masuda & Guiry (1994) for defining membership in *Platoma*, including the conspicuous intercalary gland cells and nutritive auxiliary cells. With this suite of characters now so firmly confirmed in the three best-studied members of the genus, anomalous species should now be critically re-examined. As pointed out by Masuda & Guiry (1995), these include *P. abbottiana* Norris & Bucher (1977) and *P. fanii* Dawson (1961), *P. foliosum* Womersley & Kraft (1994) and *P. australicum* Womersley *et* Kraft (1994), all of which lack gland cells and and are not definitely known to possess nutritive auxiliary cells.

Halymenia chiangiana Abbott *et* Kraft, sp. nov.

Plantae foliosae. Hapteron est tumulus incrassatus texturae cartilagineae, instar pedis equini. Stipes 1.5 cm longus, circa 0.5 cm crassus. Laminae colore sturato lateritio, consistencia solida, usque 10 cm longae et 3.5-5.5 cm late, integerae vel fere pariter bilobatae, fimbriis 2-2.5 cm profundis, crenatis, et magis divisis, raro plus quam 1 cm latis, paginis laminae acutis et obtusis projecturis. Sectio transversalis 180-250 µm crassa; cortex 35-40 µm crassus, e stratis quattuor ad sex constans, cellulis omnium stratorum praeter stratum superficiale duas vel tres fila corticalis ferenti, cellulis interioribus corticis minus quam 8 µm latis, terminalibus cellulis elongatis et 2-3 µm diam., 3-4-plo longioribus quam latioribus; subcortex compactus ex angularibus et lobatis cellulis conjunctionibus secundariis constatus; medulla laxe filamentosa, ganglioneis cellulis refractivis et dispersis, branchiis longis (tot quot 8) ad contiguas ganglioneas vel non-ganglioneas cellulas connexis; fila medullosa anticlinata pauca, ex altero cortice interiore ad alterum currentia, cellulis 2.5-6 µm diam., diametro 3-4-plo longioribus. Ampullae carpogonii angustae, parce ramosae; ampullae cellulae auxiliarium plus fruticosae, generaliter latas ad apicem, ostiolum distinctum subtentes, cellula auxiliari intercalari in primario vel secundario filo ampullae. Filum conjunctivium ad cellulam auxiliarem conjunctionem lateralem faciens et non crecens porro. Cystocarpia circa 125 µm ex duobus vel pluribus gonimolobis maturescentibus invicem constata, cellula auxiliari cum continguis cellulis ampullae non conjugenti lateraliter. Tetrasporangia cruciatim divisa, ovoidea, 10-13 µm diam., 17-25 µm longitudine, ad cellulas interiores corticis basaliter affixa et inter modificata fila anticlinata dispersa.

Plants foliose. Holdfast single, tenacious, shaped like a wooden peg or horse's foot. Stipe to 1.5 cm high, about 5 mm thick. Blades deep brick-red in color, firm in texture, to 10 cm in length by 3.5-5.5 cm in width, entire or divided between two nearly equal lobes, the margins incised to 2-2.5 cm deep, crenate and further divided, the proliferations rarely > 1 cm broad, the blade surfaces densely covered with pointed to blunt projections. Cross-sections 180-250 µm thick; cortex 35-40 µm thick, 4-6-layered, the cells of all but the surface layer each subtending 2-3 cortical filaments; inner cells of cortex <8 µm broad, the terminal cells elongate and 2-3 µm in diam., 3-4 times longer than wide; sub-cortex a mixture of delicate periclinal filaments and rounded cells that produce the filaments, the medulla laxly filamentous and with scattered, refractive ganglioid cells with as many as 8 long arms connecting to contiguous ganglioid or non-ganglioid cells; anticlinal medullary filaments few, extending across the medulla from one inner cortex to the other, the cells 2.5-6 µm in diam., length: width ratios 3-4:1. Carpogonial ampullae narrow, sparingly branched; auxiliary-cell ampullae bushier, generally broad across the top and subtending a distinct ostiole, the auxiliary cell intercalary in the primary or a secondary ampullar filament. Connecting filaments making a lateral contact to the auxiliary cell and not growing on to effect further diploidizations. Cystocarps ca. 125 µm in diam., composed of two or more successively maturing gonimolobes to 75 µm in diam., the auxiliary cell not fusing laterally with adjacent ampullar cells. Tetrasporangia cruciately divided, ovoid, 10-13 µm wide by 17-25 µm in length, basally attached to inner cells of the cortex and scattered within a palisade of modified anticlinal filaments.

Etymology. This species is named in honor of Professor Young-Meng Chiang of the Institute of Oceanography, National Taiwan University, in recognition of his pioneering studies of the genera (principally based on their type species) in the family Halymeniaceae (Chiang, 1970) and other western-Pacific Rhodophyta. We wish him well in his retirement.

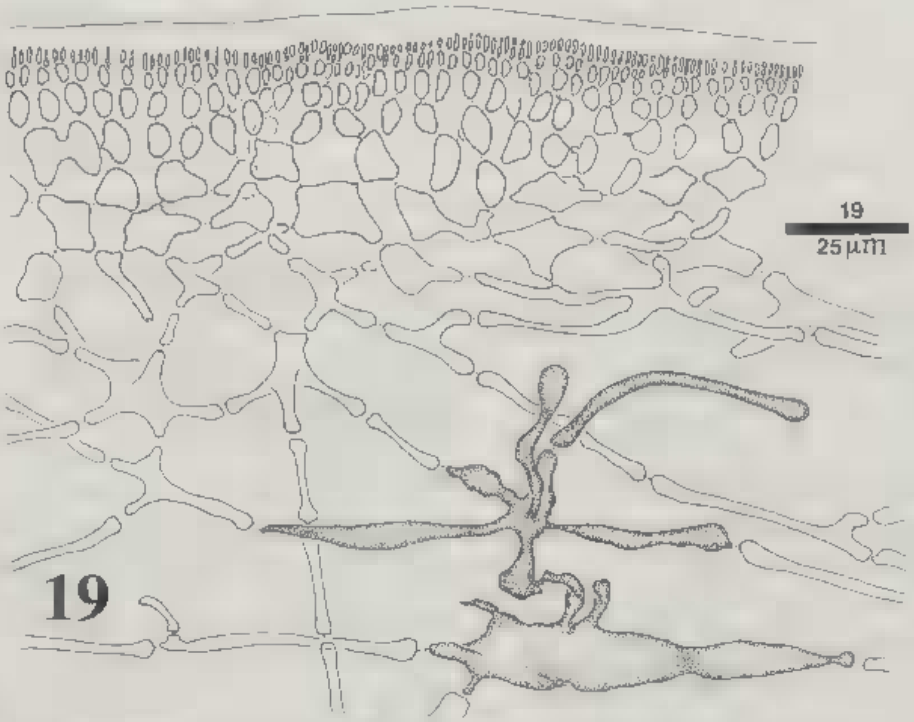
Holotype. BISH 646030, IA 22675 (Fig. 17), a cystocarpic specimen collected on 23 November 1995 by I.A. Abbott and L.M. Hodgson.

Habitat. The cystocarpic holotype and the tetrasporangial syntype specimens were collected from drift at Kanaha Beach Park, Kahului, Maui I. An *in situ* collection from the same locality was made from the reef flat at 5 m depth.

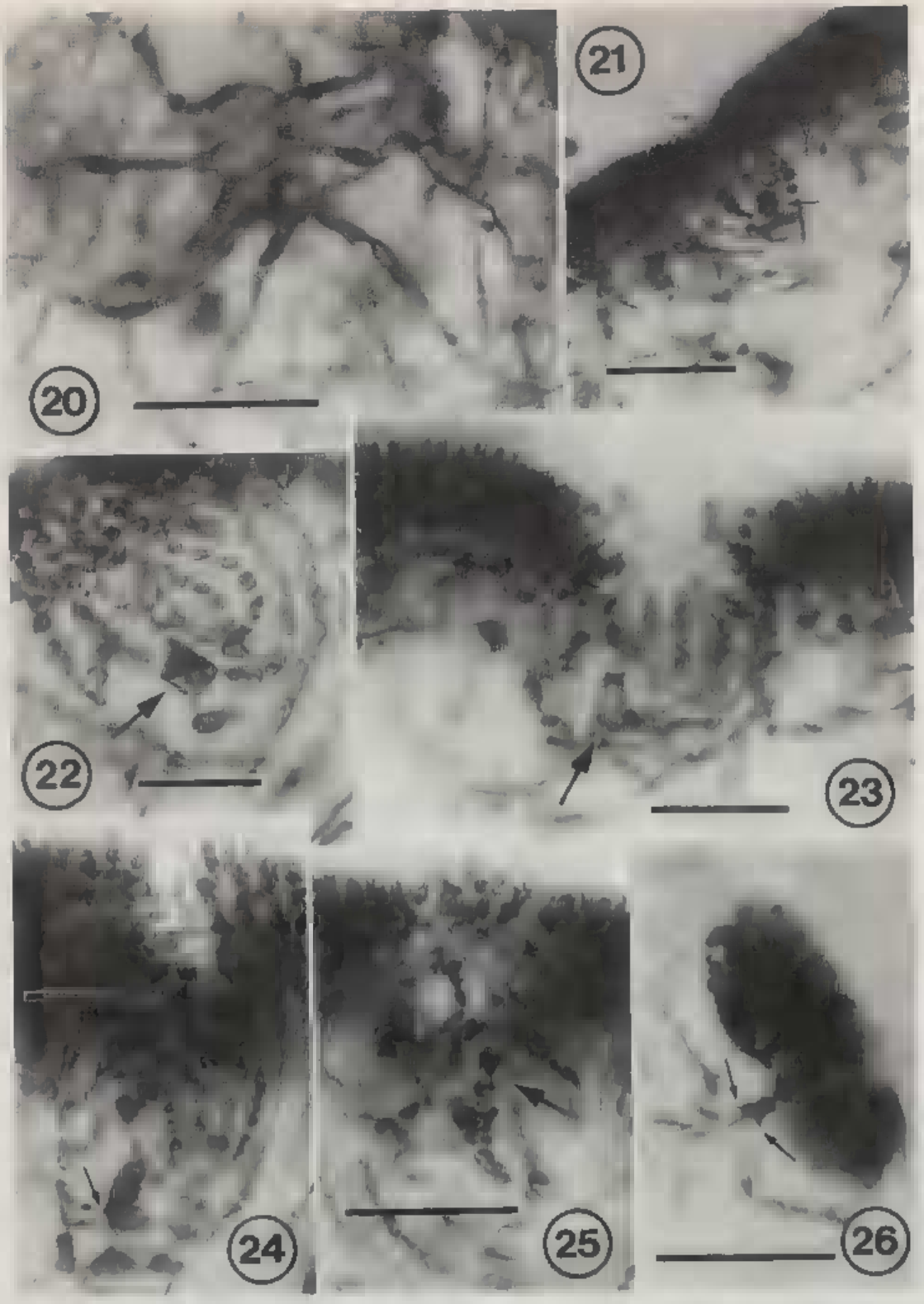
Hawaiian distribution. Maui I., Kanaha Beach Park, Kahului, Maui I., drift (*I.A. Abbott & L.M. Hodgson*, 23-24.xi.1995. *I.A. Abbott* 22676; cystocarpic); 5 m depth on coral rubble (*L.M. Hodgson*, 4.i.1996. *I.A. Abbott* 22760; tetrasporangial).

World distribution. Recorded only from the Hawaiian Islands.

Vegetative structure. The blade of the tetrasporophyte is the only entire plant in the collections. It arises from an asymmetrical, fleshy holdfast shaped like a horse's hoof and flares out from a compressed stipe 1.5 cm in length by 5 mm in thickness. The blade is firm-textured, 10 cm in length by 3.5-5.5 cm in width, and either entire or divided into two roughly equal lobes in the case of the tetrasporophyte, or consists of a single prominently lobed fragment in the female gametophyte (Fig. 17). Margins are variously smooth, broadly proliferous or finely dentate (Figs 17, 18). The entire surface of both plants is covered with subacute, broadly rounded and irregularly peltate lobes and excrescences that reach 1 cm in height and width. Occurring on many of the furrows and lobes are large numbers of smaller, harder projections (Fig. 18), many of which are associated with masses of roughly 0.5-1.0 µm diameter particles that may be evidence of localized bacterial infection. Blade cross-sections range from 180-250 µm in thickness exclusive of



Figs 17-19: *Halymenia chiangiana* Abbott *et* Kraft sp. nov. Fig. 17. Habit of the cystocarpic holotype specimen (BISH, IA.). About natural size. Fig. 18. Detail of one of the thallus lobes showing dentate marginal processes, major ridges and lobes, and numbers of small excresences that may be at least partially responses to bacterial infections. Magnification is about 2x. Fig. 19. Cross section of cortex and central medulla, showing two refractive "ganglioid" cells in the medulla, stellate cells in the inner cortex, and a direct lateral fusion between two of the mid-cortical cells.



Figs 20-26: *Halymenia chiangiana* Abbott *et* Kraft sp. nov. Fig. 20. A large ganglioid cell from the medulla. Scale = 100 µm. Fig. 21. An auxiliary-cell ampulla with prominent auxiliary cell (arrow) projecting into the medulla. Scale = 100 µm. Fig. 22. The moniliform, sparingly branched filaments of an auxiliary-cell ampulla, the auxiliary cell (arrow) the basal cell of a first-order lateral. Scale = 50 µm. Fig. 23. An auxiliary cell (arrow) in a mature ampulla, the ampulla broad and subtending an ostiole in the cortex. Scale = 50 µm. Fig. 24. An auxiliary cell at or near diploidization, a connecting filament (arrow) fused to a lateral surface. Scale = 50 µm. Fig. 25. The gonimoblast initial (arrow) directed toward the ostiole above the diploidized auxiliary cell. Scale = 50 µm. Fig. 26. Oblique view of a mature carposporophyte attached to an auxiliary cell that is unfused (arrows) to the contiguous ampullar cells. Scale = 50 µm.

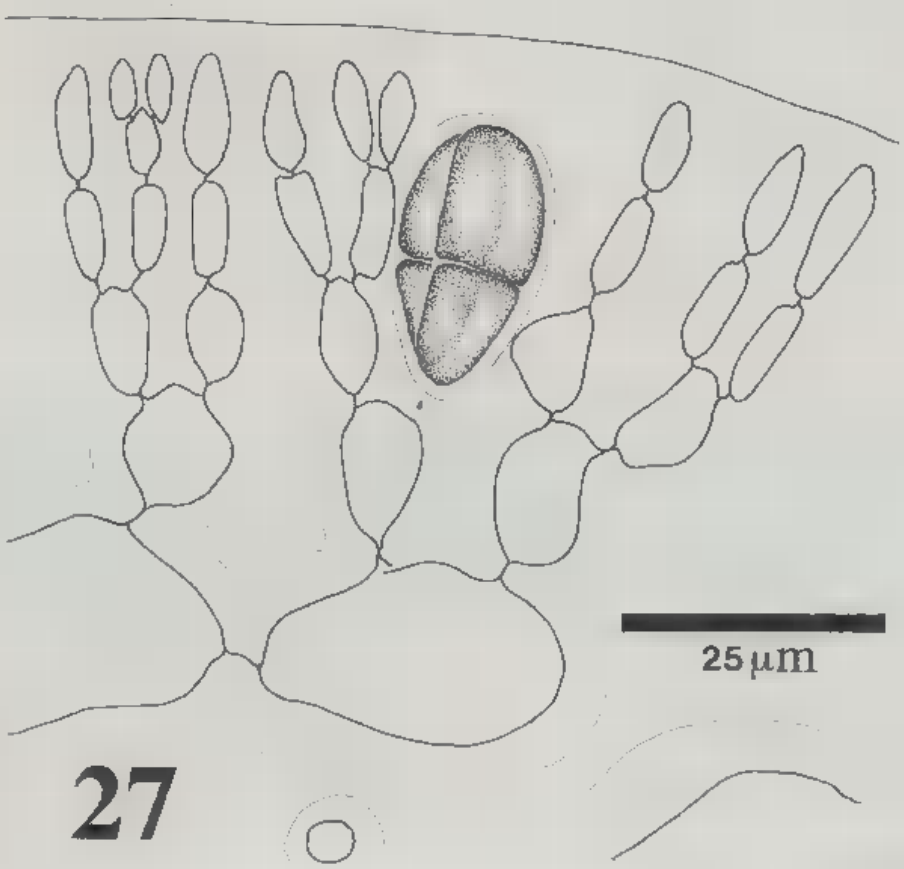


Fig. 27: *Halymenia chiangiana* Abbott *et* Kraft sp. nov. Cortex section showing basally attached, cruciate tetrasporangium borne in a palisade of anticlinal outer cortical filaments.

the surface projections and are comprised of a broad and laxly filamentous medulla consisting of mostly periclinal filaments but also including numbers of anticlinal filaments that traverse the medulla from inner cortex to inner cortex. Of frequent occurrence in the medulla are irregularly contoured, enlarged cells with numbers of slender, radiating arms and highly stainable, refractive contents (Figs 19, 20) that are termed by Womersley & Lewis (1994) "ganglionic" cells. Cells at the border of the medulla and cortex stain normally and are often stellate in configuration (Fig. 19). External to the stellate layers is a cortex 35-40 µm thick composed of 4-6 layers, the cells of the inner layers ca. 8 µm in diam and frequently secondarily pit-connected, at times also laterally fusing (Fig. 19). Surface cortical cells are elongate, 2-3 µm in diam. by 6-12 µm in length.

Reproduction. Plants are apparently dioecious, as spermatangia have not been observed. The structure of carpogonial ampullae has not been clear, as carpogonial branches apparently are extremely evanescent. Auxiliary-cell ampullae protrude from the inner cortex into the medulla (Fig. 21) and consist of moniliform filaments branched to the second or third order (Fig. 22) with the auxiliary cell intercalary and basal in a second-order filament. The mature ampulla is broader than long, flat-topped, and situated at the

base of an ostiole that is fully developed prior to diploidization of the auxiliary cell (Fig. 23). Connecting filaments have not persisted after diploidization in our material but appear to fuse laterally with the auxiliary cell and not to grow beyond it. The auxiliary cell just subsequent to diploidization elongates toward the ostiolar pore (Fig. 24) and cuts off a single, distal gonimoblast initial (Fig. 25), the carposporophyte then forming two or three synchronously developing gonimolobes within a lax involucre of surrounding and elongating ampullar filaments. The carposporophyte reaches 125 µm in diameter and is anchored to an auxiliary cell that does not enlarge appreciably or fuse to any extent with contiguous ampullar cells (Fig. 26).

Tetrasporangia (Fig. 27) are ovoid, 17-25 µm in length by 10-13 µm in width, and basally attached to bearing cells that lie at the base of a thickened, anticlinal cortex covering much of the fertile frond.

DISCUSSION

The new species has many of the features described by Kawaguchi (1987) for *Halymenia dilatata* Zanardini from Japan. Both species arise from short stalks, have irregularly lobed to oblong fronds, a similarly composed cortex and ganglionic medullary cells. *Halymenia dilatata* is commonly also proliferous from the surface. Auxiliary-cell ampullae are similar in morphology and equally subtend a broad ostiole prior to diploidization in both species. Although Kawaguchi (1987, fig. 4D) illustrates connecting filaments that enter and leave the auxiliary cell, he notes Balakrishnan's (1961) observation that this feature was variable in Indian material, in which the connecting filaments most often terminated at the auxiliary cell. Differences between the species include the much greater numbers and blunter surface proliferations of *H. chiangiana*, its thinner fronds (to 250 µm vs 350-400 µm), its lack of deeply pigmented surface spots (maculae), and its unmodified tetrasporangial cortex.

Compared to other genera in the Halymeniaceae, this, the type genus, has received relatively little attention. In trying to frame a definition, Abbott (1967) emphasized the traversing, or anticlinal, medullary filaments as a primary diagnostic feature, as did Kraft (1977) and Maggs & Guiry (1982). Abbott (1967) also highlighted the ganglionic cells of the outer medulla, as have Womersley & Lewis (1994), who point out that although highly refractive ganglionic cells seem to be absent in some species (e.g. *H. kraftii*), the stellate cells that seem to be their precursors are consistently present. Womersley & Lewis (1994) re-iterate the observation of most students of *Halymenia* that the cortex is "relatively narrow". Chiang (1970) called particular attention to the distinctive *Halymenia*-type ampulla, with its "flattish and expanded" profile, a feature repeatedly confirmed by other workers (Acleto, 1973; Codomier, 1972; Maggs & Guiry, 1982) and thought by Kawaguchi (1987) to be perhaps the most consistent and reliable generic character. The importance of ampullae and of ampullar types is now being re-assessed, this feature having been downgraded by Kraft (1977) and Maggs & Guiry (1982) but now coming once again to be more heavily weighed in recent taxonomic treatments of the family (Kawaguchi, 1993, 1997), particularly in regard to a number of species now being placed in or removed from *Grateloupia* (Kawaguchi, 1991; Lee *et al.*, 1997).

The leading student of the Australian Halymeniaceae, John A. Lewis, has concurred (pers. comm.) with our suggestion that the lack or near lack of major ampullar-cell fusions to the auxiliary cell during gonimoblast maturation in *Halymenia* may also constitute a reliable generic feature, one consistently differing from typical *Grateloupia*

species (Kawaguchi, 1997). Only extended comparisons of *Halymenia* species will confirm or refute the stability of this and other generic characters, but it is clear that the new Hawaiian species described here conforms to our present understanding of *Halymenia* in all its essentials.

The two new algae that we describe here exemplify superficial habit similarities that can occur in species that are only distantly related at best. Recent molecular investigations (Saunders & Kraft, 1996) have not fully resolved the place of members of the Schizymeniaceae, although indications are that they form a group at the base of the gigartinalean clade. The Halymeniaceae, on the other hand, belongs to a monophyletic group well distinct from the Gigartinales and as such has recently been placed in the separate order Halymeniales (Saunders & Kraft 1996).

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